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STUDIES IN THE GENUS GYMNOSPORANGIUM IV. DISTRIBUTION OF THE MYCELIUM AND THE SUBCUTICULAR ORIGIN OF THE TELIUM IN *G. CLAVIPES*

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A parasitic fungus in its periods of exploration and attack seeks out those regions where its essential foods are readily available. The host may react to the irritations in such a way as to lead to the formation of abnormal growths which can be relied on in diagnosing the disease. Most species of Gymnosporangium are, aside from their morphological differences, easily distinguished, because each species may differ from the others not only as to the tissues invaded but also as to the manner of the attack.[1] *G. clavipes* Cke. & Pk. on *Juniperus virginiana* differs from all other species studied by the writer in the very limited or superficial way in which the mycelium invades the host, and in the location of the telial sorus as it is formed in leaves or young stems. Hitherto it has been thought that the telia of all Gymnosporangia arise beneath the epidermis. Those of *G. clavipes* are not subepidermal but are developed in the outer wall of the epidermal cells. They might be called *subcuticular*, but, as will be noted later, there is no single word in English that is strictly applicable.

Ducomet[2] made a special study of those spot-disease fungi which live at least a part of the time beneath the cuticle of the host. The method of invasion by such fungi is quite as characteristic as the location of the spore-bearing structures with respect to the cuticle or epidermis. Ducomet found that certain species develop directly beneath the cuticle. These would be called subcuticular in a strict sense. Other species develop in the outer wall of the epidermal cells, in that part which is known as the cuticular layer and which is composed of cellulose and cutin. He proposes such names as *intracuticulaire*, *subintracuticulaire*, etc., terms which do not convey very well the meaning desired.

Arthur[3] has emphasized the taxonomic importance of knowing the location of the sori in rusts.

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[1] For further discussion of this question see Wörnle, P. Anatomische Untersuchung der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forst. Nat. Zeitschr. **3** : 68–84, 128–172. 1894; Dodge, B. O. Studies in the genus Gymnosporangium I. Notes on the distribution of the mycelium and the germination of the aecidiospore. Brooklyn Bot. Gard. Mem. **1**: 128–140. 1918.

[2] Recherches sur le développement de quelques champignons parasites à thalle subcuticulaire. 1907.

[3] Résult. Sci. Congr. Bot. Vienne, p. 333. 1906.

> Im allgemeinen zeigt die Tiefe in den Geweben des Wirtes, den sich der Pilz zum Sitz seines Lagers ausgewählt hat, eine gewisse Beziehung zu der phylogenetischen Entwicklung.

In certain subfamilies pycnia are always subcuticular, other sori may or may not be so situated. In several genera all sori are subepidermal.

Grove[4] also believes that the placement of sori is an indication of the trend of evolution. The transference of the spores to a place either (1) beneath the cuticle, (2) in the epidermal cells, or (3) just beneath the epidermis, and their aggregation into definite sori would be advances in adaptation, "and the most effective of all (the subepidermal sorus) is alone to be met in the highest groups."

The writer[5] investigated the origin of the teliospore in several of our common Gymnosporangia and found that here, unlike the condition in all other known rusts, the teliospores are formed from buds arising out of subterminal cells of the plectenchymatous primordium. After discovering that the telial sorus of *G. clavipes* is subcuticular, it was thought that it might differ in the origin of the teliospore from other Gymnosporangia and thus conform to the mode described for all other rusts. However, as will be shown later, here too the preteliospore degenerates, functioning only as a buffer cell just as it does in the other forms previously described by the writer.

The Host–Parasite Relationship

The first leaves of the actively growing shoot of the young red cedar are called subulate in contrast with the scale leaves formed later. The free blade is somewhat less than a centimeter long and the basal portion runs down on the stem about the same distance, varying according to the rate of growth of the stem. As there are three rows of leaves, a cross section of the stem shows the three decurrent leaf-base ridges. The parenchyma of these leaf ridges merges with that of the cortex of the stem, so that there is frequently no definite separating line (Pl. XXII, fig. 3).

The leaf is provided with stomata along its upper (proaxial) surface and on the abaxial side downward from a line about opposite the end of the resin duct, or a little above the line of the leaf axis. There is a single vein in the leaf. A layer, one or two cells thick, of stereome extends along the lower side next the epidermis and continues down the decurrent basal portion, being interrupted wherever stomata are present.

In addition to the true cuticle, the common covering of the leaf and young stem, the epidermal cells are further provided with a layer which can easily be differentiated by proper staining. According to Von Mohl,[6] the cuticular (cuticularized) layer as distinct from the true cuticle is that part of the wall of the cell which has a cellulose matrix impregnated with cutin. Irregular tooth-like projections alternate with notches and pits of a different consistency, so that this region appears more or less porous or granular. The cuticular layer is thickest on the outer wall of the cell, but it extends down between the epidermal cells some distance, and may even occur along the inner wall.

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[4] The British rust fungi, p. 79. 1913.

[5] Mycologia **10** : 182–193. 1918.

[6] Bot. Zeit., p. 502. 1847.

The epidermal cells of the cedar are oblong or brick-shaped, easily distinguished from the palisade mesophyll on the upper or proaxial side of the leaf. Other features necessary to the ready understanding of the pathological aspects of the subject are brought out by figures in the text and plate.

Infection experiments and field observations made during a number of years indicate that the first telia of *G. clavipes* on *Juniperus virginiana* are formed either directly on the leaves or, more commonly, at the margins of the decurrent leaf bases or in leaf axils of branches not over two or three years old. Later, as cork is laid down, sori break through in the ordinary manner. We shall therefore follow here the course of the fungus during the first year or two of its life in the host.

The Mycelium in the Leaf

Infection takes place on the proaxial side of the young leaf, or directly on the young stem at the base of the leaf. Primary infection can not occur

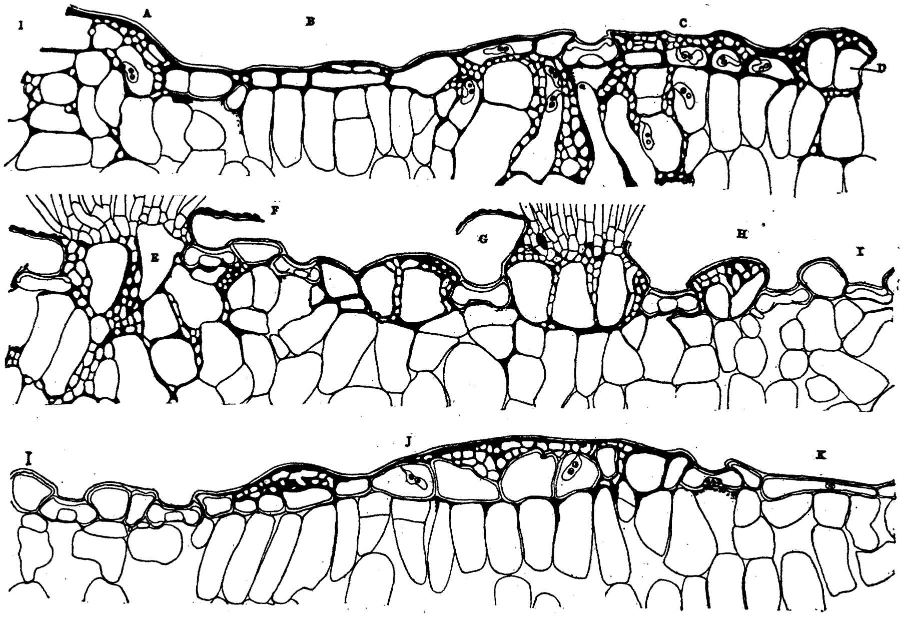

FIG. 1. *A* to *K*, portions of longitudinal section of a leaf of red cedar infected with *Gymnosporangium clavipes;* shows two sori and the manner of advance of the mycelium. Intercellular hyphae have penetrated little beyond the palisade cells, which in many cases have been stimulated to divide. See text for further description.

on stems protected by a layer of cork cells. The mycelium may be confined to the leaf two or three years, developing sori each season; the leaf may then die off without the fungus having been able to reach the stem tissues below. After entering the leaf, the mycelium invades the region between the cuticle and the cellulose walls of the epidermis on the proaxial side. The effect of the fungus on this part of the cell wall is usually marked by considerable swelling, and the disorganized substances take the stains very readily (indicated by shaded portions in my figures). The cell walls of the hyphae also thicken so that it is often difficult to say where these end and the disorganized cuticularized region of the host begins. Haustoria are found in epidermal cells (fig. 1, *C*), sometimes even in the guard cells of stomata. As noted, the fungus explores and feeds in the cuticularized layer, but it may go deeper and invade the palisade mesophyll tissue. None of my sections shows hyphae on the abaxial side of the leaf. Figure 1, *A* to *K*, represents about three fifths of that portion of the leaf which shows the presence of the fungus. Hyphae are found near the epidermis along half the entire length of the leaf. At *A*, palisade cells have divided and the epidermal cells are swollen. At *B*, only a few hyphae are visible but beneath the stoma the mycelium is massed between the palisade cells. The cuticle is raised considerably at *C*, and the cuticularized layer beneath it is much disorganized. At *D*, there is a swollen supporting cell of the stoma which is shown at the left below. Exploration laterally in the cutinized wall is very slow.

At *E* in figure 4 the epidermis is normal. All traces of the fungus in this section are indicated in the figure, and it is evident that no hyphae approach the conducting system *F*. The attack on the leaf is certainly very limited and superficial, but not more so than it is on the young stems or old tree trunks, phases which will now be considered.

Distribution of the Mycelium in Young Stems

Vigorously growing terminal regions of young stems are the most susceptible to infection, either directly or through the invasion of the fungus by way of the leaf axils. At the time of the formation of the first sori, which will be either about ten months or a year and ten months after infection, the stem will still be green and devoid of cork tissue, the greater portion being covered by the decurrent leaf bases. The diagrams *A–F* in figure 2 were made from a series of sections of a small branch of plant no. 403 which had been infected in August, 1915,[7] the first sori appearing in the spring of 1917. The number of sections 7 μ thick between those diagramed is given in the figure. Beginning with diagram *A*, the mycelium represented by shading is shown to occupy the three regions in the cortex between the decurrent leaf bases (*L*), not approaching the cambium; even the phloem tissue is some distance beyond. Passing up the stem about

[7] See Bull. Torrey Bot. Club **45** : 287–300. 1918.

a millimeter, diagram *B* shows that each mycelial strand is being broken up or split as a new set of leaf bases (*L′*) appear. Only a tenth of a millimeter farther (*C*) we find that each strand has been completely split and that there are now six distinct regions in the cortex penetrated by the fungus, a pair of mycelial strands for each leaf base. At *D* hyphae have cut in beneath one leaf vein, and the union of the members of the other two pairs of hyphal strands is completed thirty-three sections above at *E*. Note that there is some mycelium invading the epidermis on the proaxial side of the leaves near the lines of attachment. At the point *F*, a few sections above, two leaf blades are detached, and subcuticular and intercellular hyphae have penetrated still farther into the leaves. The last of these hyphae is seen in the twentieth section (not shown) above *F*, proving that the mycelium penetrated only 210 μ into the leaf above the line of its attachment to the stem. These gaps between strands of mycelium continue up and down stems even in those showing three rings of wood, and one wonders if the fungus would ever occupy the entire cortex, especially as he finds old trunk infections confined to only a small part of the circumference. But in an infection such as the one diagramed in figure 2 the strands actually interlace, weaving in and out around the veins of the leaves and forming a closed network system in the cortical region of the

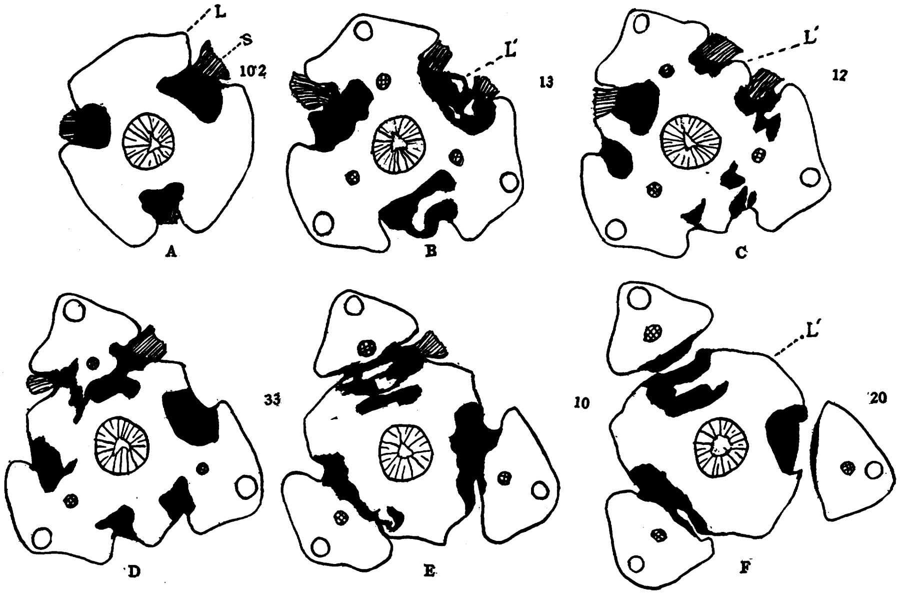

FIG. 2. Diagrams *A* to *F* made from cross sections of a branch infected with *Gymnosporangium clavipes*, Aug., 1915, cut March, 1917. Shaded portions show location of mycelium and sori. A longitudinal diagram would have shown these mycelial strands interlacing, forming a closed network as they weave around the veins leading into the leaves. See text for explanation and discussion.

young stem. After the leaves are shed, the fungus, closing the gaps, will be found in the cortex around the entire circumference of every section. The diagrams bring out very strikingly the fact that the mycelium never gets very near the conducting systems of the host. Wörnle (*l.c.*) states that he found mycelium of *G. clavipes* in the bast. He was apparently mistaken in this regard, as I have seldom if ever found hyphae approaching phloem very closely.

The Mycelium in Trunk Infections

The fungus at first advances longitudinally in the stem one to three centimeters each year but circles it very slowly, sometimes taking several years in the process. In many cases of trunk infection the mycelium is always confined to a small region and never completely girdles the tree. Where the stem is attacked in a rapidly growing region, such as at the end of the main axis or at the tip of a well exposed branch, the fungus is outstripped by the host, the infection being recognizable in later years by the slightly fusiform swelling. If infection takes place on a slowly growing side branch, the parasite grows upward with the host, penetrating new branches, frequently causing, as a consequence, distortions like small witches' brooms.

The main trunk of the cedar may also become infected, even after many layers of cork have been laid down, as a result of the downward growth of hyphae from an infected branch. Such secondary infections may account for the types of injury characterized by black patches a few inches in diameter on trunks of large trees, showing how little damage may be caused by this species during the fifty or one hundred years which have passed since infection occurred.

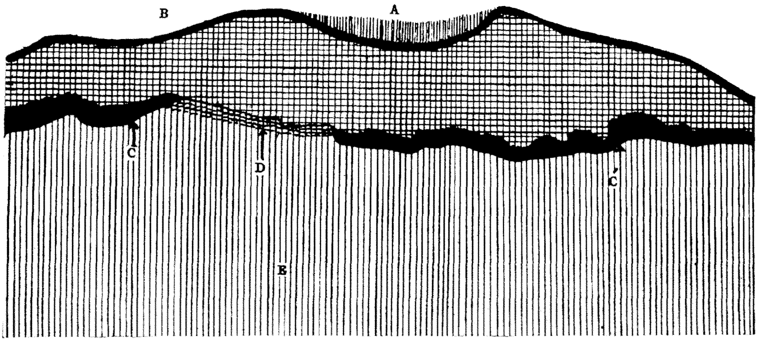

FIG. 3. Diagram representing a small portion of the cortex, Nov. 25, 1917, of an infected cedar limb twenty years old, showing the manner in which the wound callus cuts off the old sorus and adjacent infected tissue of the preceding spring. *A*, remains of teliospore stalks. *B*, wound callus cork. *C*, cork cambium and one or two layers on either side among the cells of which hyphae have invaded from the margins. *D*, uninfected gap of cork cambium which will soon be invaded. *E*, uninfected cortex, which extends much farther down.

A good demonstration of the presence of the fungus in the cedar can be made from free-hand sections. Fixed with Flemming's agent, the invaded tissues are blackened so that one sees a narrow ring consisting of phellogen and one or two adjacent rows of cells just below the cork, perhaps not over 5 to 10 percent of the cortical zone (Pl. XXII, fig. 5, and text fig. 3). Bleached and stained with the triple stain, characteristic binucleated haustoria and hyphae become visible. It is undoubtedly the vigorous attack on the phellogen cells by the fungus that prevents the formation of the normal amount of cork. As soon as the spores have germinated in the spring a new cork cambium is developed in the cortex beneath the sorus, so that as the callus is formed all traces of the fungus disappear as last year's infected tissue is lifted up and sloughed off. This would leave pockets in the cortex beneath each old sorus devoid of fungus were it not for the reëntrance of the parasite from the sides (*C*, *C'* , fig. 3). The diagram represents this condition, Nov. 25, 1917, in a small area from an infected limb twenty years old. Remains of the old telium (*A*) are still visible above the wound callus. There is a small region (*D*) of phellogen still free from the parasite. Now, if this infected area had been examined in April of the preceding spring, the hyphae beneath the sorus would have been confined to the region of the cork cambium as shown in figure 4, Plate XXII. While, as stated, hyphae in such infections usually occupy only the two or three outermost layers of the living cortex (Pl. XXII, fig. 5), yet one often finds the fungus halfway down to the phloem.

THE ORIGIN OF THE SORUS

The telial sorus may be said to originate in that region where the spore buds are formed. The sorus of *G. clavipes* would be subcuticular in a broad sense because the subterminal cells in the plectenchymatous primordium are formed in the cuticularized layer of the host, which would be somewhere between the cuticle and the lumen of the epidermal cell beneath.

The Telium in the Leaf

In view of the very superficial attack on the leaf and young stem tissues by the fungus, which appears to get much of its nourishment from the epidermis, it does not seem strange that the sorus primordium should be found originating in the cuticularized layer. The point at which a sorus will develop is usually marked by a massing of hyphae, so that the cuticle is widely separated from the underlying cells (fig. 4, *D*). As the primordium enlarges and spores are formed, the cuticle, carrying some portion of the cuticularized layer which has become more or less disorganized, breaks away along a line and folds back so that the nature of the sorus can be determined very readily. A small sorus is shown at *E*, figure 1, where the mycelium is deep-seated. The large cells (*E*) at the base of the sorus are the supporting cells of the stomata on either side. Another sorus is shown at *G*. Hyphae pass around the stoma, showing in this section again at *H*, where both supporting epidermal cells are enlarged. The effect of the fungus near by is seen at *I*, hyphae appearing again in the section exploring new regions subcuticularly toward *J*. The epidermal cell at *K* is normal; no hyphae have advanced beyond this point in the leaf.

The nature of the telium is even more evident in the cross section outlined in figure 5, where the epidermal layer is still unbroken from the stoma at the left to the limits of the sorus at the right. The cells of the epidermis are somewhat swollen, but 70 μ farther up some of them are nearly normal (fig. 6). Hyphae have crowded in between the longitudinal rows of epidermal cells at *A*, and two of these have been shoved aside, but they can be seen in the adjacent sections of the slide.

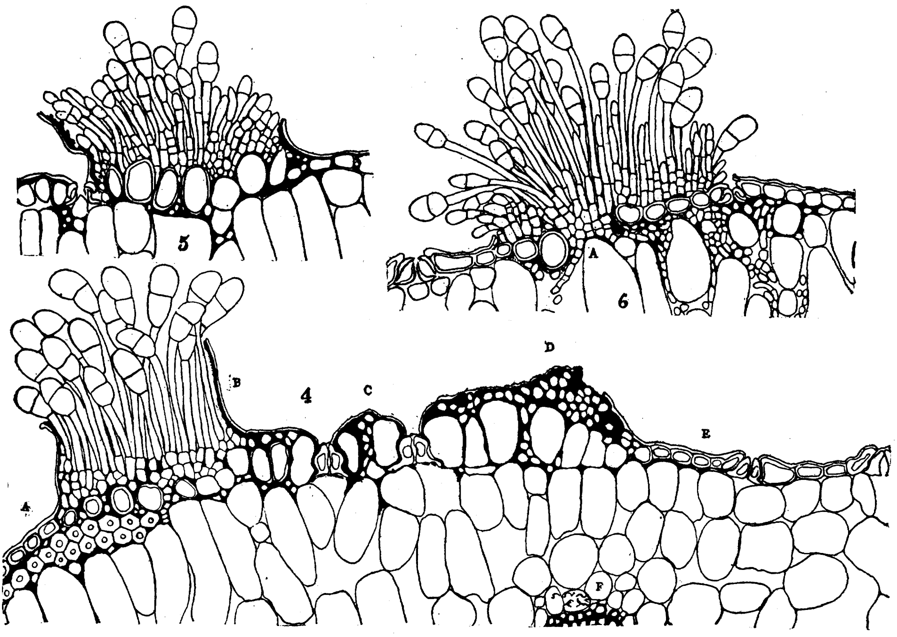

FIG. 4. Part of a cross section of a leaf at the margin, showing a sorus above the epidermal layer, which is continuous. See also text. FIG. 5. Cross section of a portion of leaf through a sorus. The epidermal layer is unbroken, but the cells are swollen. The sorus originates between the cuticle and the epidermis. FIG. 6. Section of the same sorus 70 μ above. Mycelium has pushed in between the epidermal cells at *A*. Very little hypertrophy of the epidermal cells beneath the sorus here.

It sometimes happens, especially in sections cut rather thick, that the portion of the cuticle raised above the sorus, and to which cling some of the disorganized remains of the cutinized walls of the epidermal cells, becomes turned over by pressure on the cover glass so that one is very likely to be misled into thinking that the sorus is really subepidermal or intra-epidermal because what appear to be portions of the epidermis lie above the sorus. The corrosive effect of the hyphae, especially of the buffer cells, on the cuticularized layer is such that indentations or notches are left in the layer which, as noted, clings to the cuticle finally raised above the sorus. These markings are all the more misleading inasmuch as the outlines of the epidermal cells also persist in the raised portion, because the cuticularized part of the walls extends down between the epidermal cells, forming a sort of cap. One can readily show that there are two sets of markings or notches in the portion raised above the sorus by photographing oblique sections of a mound-shaped sorus. Such a surface view is shown in Plate XXII, figure 8. Unquestionably additional nourishment for spore formation may come from the mycelium in the mesophyll, and it is not impossible that hyphae present in this region may push up between the epidermal cells to form the telial stroma in the cuticular layer. Such a sorus would not, however, be subepidermal. The red cedar leaf is strengthened by stereome tissue at the edge as shown below *A* in figure 4. Nothing but epidermal cells lies above this stereome, and the epidermal layer is unbroken under this sorus from *A* to *E*, although at *C* and *D* its cells are hypertrophied.

The Sorus in Young Stems

When young stems are infected, sori appear at the margins of the leaf bases or in the axils. It is unnecessary to describe in detail the development of the sorus, as the epidermis, provided with stomata, persists for two or three years and the sorus is formed in the cuticular layer just as it is in the leaf. It is much more difficult to trace the unbroken epidermis beneath the sorus because of the great irregularity of the cells in the region of the leaf axils where the epidermal cells are normally very large, often pointed, and frequently separated by intercellular spaces. In an infected stem these cells are generally still further enlarged and come to look like cortex cells, especially as they are pushed aside or displaced by the invading strands of mycelium. In no case has there been found the slightest evidence that the sorus is subepidermal. Figure 7 shows a portion of a sorus on a young stem, the raised cuticle carrying a part of the cuticularized wall of the epidermal cells appearing at the right.

It is an important point to determine just where the sorus originates, although it is the morphology of the fungus and not the host-parasite relation that determines its place in a classification. This relationship, however, may very often indicate special adaptations developed in the course of evolution, and as such may be characteristic of a number of species in a given group.

The writer is indebted to Professor J. C. Arthur and Dr. J. F. Adams for criticisms written after an examination of some of the preparations, and in line with their suggestions there has been an attempt to describe still more clearly the exact nature of the origin of the telial sorus of this unique Gymnosporangium.

Prof. Arthur writes that he thinks my use of the term *subcuticular* is misleading and suggests the term *superepidermal* as more accurately describing the location of the telium of this species. After examining a number of species of rusts having "*subcuticular*" sori I am convinced that much further careful work along this line is desirable. It is possible that the introduction of the new term will be found advantageous and even necessary. For example, preparations of young material of *Peridermium Peckii*, *P. balsameum*, *P. Hydrangeae*, and *Caeoma abietis-canadensis*, loaned by Dr. Adams, seem to show that the pycnia of these forms arise in the cuticular layer of the host in the same way that the telium of *Gymnosporangium clavipes* is developed, and that in the first two forms the epidermis entirely disappears beneath the mature pycnium. The pycnia of these forms have always been described as subcuticular,[8] and it is in this broad sense that the term has been used in this paper.

It should have been noted that as the sorus of *G. clavipes* ages the walls of the epidermal cells frequently disappear and the massing of hyphae continues until one can find gaps in sections where no epidermal cells separate the sorus from the mesophyll. This condition is due either to the gradual absorption or crushing down of the original cells or to the wide separation of them as noted previously in connection with figure 6 at *A*.

THE ORIGIN OF THE TELIOSPORE

It was found that the teliospore buds of *G. clavipes* on trunks or cork-covered branches arise from subterminal cells of the basal primordium, agreeing in this respect with the other species previously studied by the writer. It then became a matter of interest to learn how the spores arise in the primary or first sori, which always occur on leaf blades or on young stems still unprovided with cork. The rapid maturation of spore initials, the mucilaginous degeneration products surrounding cells and the cuticularized layer, and the natural tendency of the spore walls to swell, all contribute to make it somewhat difficult to obtain sections showing clearly a series of stages in the origin of the spores.

If one follows the development of the terminal or buffer cells in a very small leaf sorus, he will see that the cuticle is apparently very much stretched and remains unbroken for some time. Fully expanded buffer cells can be found in a sorus where other terminal cells are just beginning to disorganize. Half of a small sorus at the margin of a leaf base on a young stem is shown in figure 7. At *A* the cuticle with the clinging, disorganized cuticularized layer (shaded) is pushed up. Buffer cells are degenerating, and a teliospore bud is arising from a subterminal cell. The remains of the nuclei in the terminal cell at *B* show as deeply stained masses, but the cell still contains some cytoplasm. A young teliospore adjacent to an old buffer cell is shown at C. By cutting oblique sections of somewhat larger stems, rows of terminal buffer cells can be found, raising the cuticle for some distances. In still older stems which are provided with a cork layer, the pseudoparenchymatous primordium arises from hyphae mostly confined to the phellogen layer (Pl. XXII, fig. 4). The cork is raised and broken by the buffer tissue in the manner which I have described (*l.c.*) for the effuse trunk forms of *Gymnosporangium nidus-avis.*

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[8] Ludwig, C. A. Notes on some North American rusts with Caeoma-like sori. Phytopath. **5** : 278. 1915.

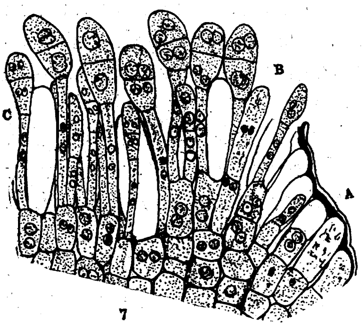

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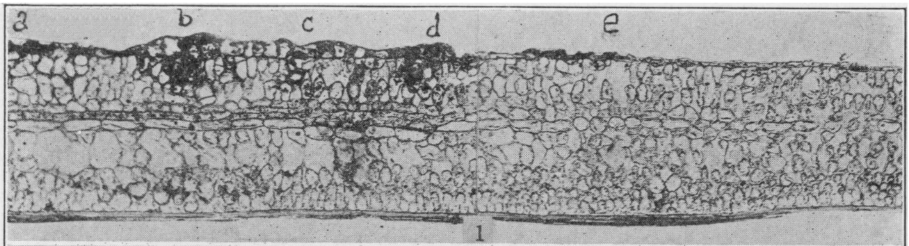
FIG. 7. Buffer cells in a sorus on a young stem at the margin of a leaf. At *A* and *B*, various stages in buffer cell formation. Teliospores arise from subterminal cells. At *C*, a young spore arising from the subterminal cell, above which can still be seen the buffer cell.

However limited may be the attack by the sporophytic stage of ~~this~~ species on Juniperus, it should be noted that it is quite the contrary case with the gametophytic mycelium in Crataegus. Here the hyphae penetrate deeply into the cortex down to the cambium, which loses its identity and ceases to function in an orderly fashion so that stereome and sieve tubes are often entirely wanting on the side of the stem invaded. The outer margin of the wood ring is irregular and indefinite. Haustoria are found in pith rays and in parenchyma cells surrounded by xylem. There seems to be no special tendency to obtain food from cells of the epidermis or phellogen, although in material cut late in the season haustoria are found in nearly every living cell. They are long, irregular, and hypha-like, branching and coiling about in the cell, quite unlike the trim, constantly binucleated haustoria of the sporophytic stage.

In cedar leaves or young stems sporophytic hyphae surround epidermal cells, attacking the cuticularized layers, and sending haustoria even into the guard cells, and it is interesting to find them in cells whose walls have become somewhat suberized. Substances related to those from which cutin is finally formed naturally occur more abundantly in these regions. In older stems provided with a cork tissue, the cells of a phellogen are certainly rich in substances undergoing a series of transformations in the layers of their walls such that by their final elaboration they may be deposited as suberin. These facts noted above might be taken as further evidence that the transition substances entering into cutin and suberin are closely allied. It is not strange, then, that this species is very limited in its attack on the host and that the first sori, *i.e.*, those on leaves and young stems, are subcuticular. A fundamental morphological feature such as the formation of buffer cells from the terminal cells in the sorus primordium is one fixed in the course of evolution and not to be easily affected by environmental conditions. Further cytological study will undoubtedly result in the dis-



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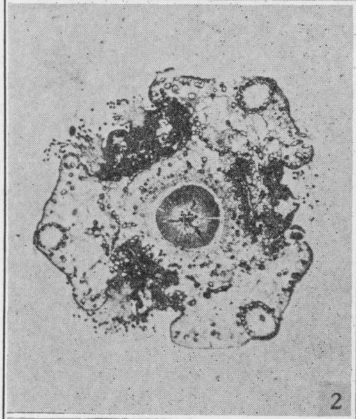

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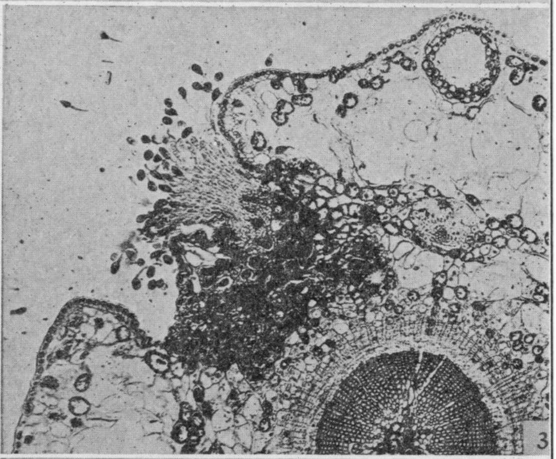

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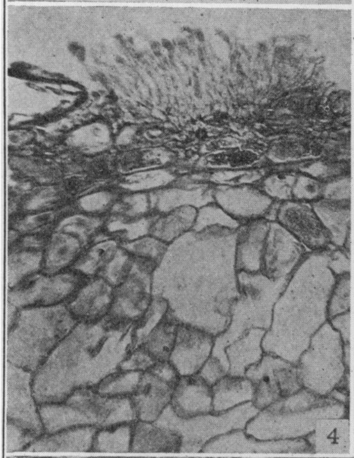

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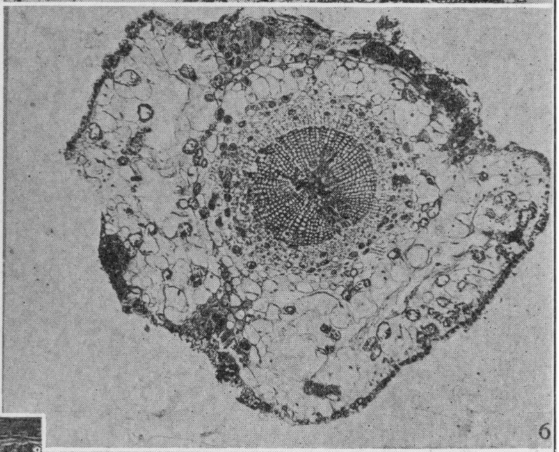

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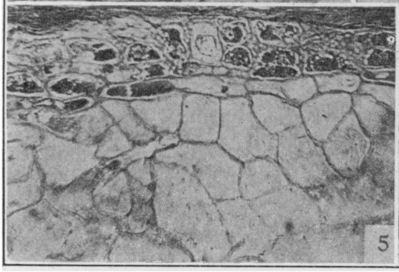

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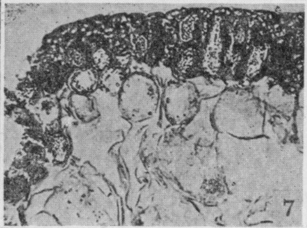

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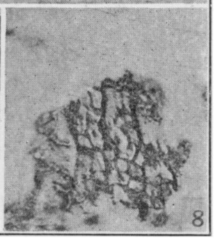

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Dodge: The Genus Gymnosporangium

covery of other rusts outside this genus whose teliospores arise from subterminal cells.

SUMMARY

The sporophytic mycelium of *Gymnosporangium clavipes* on *Juniperus virginiana* in the periods of exploration and attack is found in the cuticularized layer of the epidermal cells of the leaves and young stems. As the season advances the hyphae penetrate into the mesophyll. In cork-covered stems the parasite is generally confined to the two or three outermost layers of cells of the living cortex, although hyphae are sometimes found much nearer the phloem. Characteristic binucleated haustoria occur in the cells of the epidermis and mesophyll.

The first sori always appear either directly on the leaves or, more commonly, on the stems at the margins of the decurrent leaf bases or in the leaf axils. In later years, as cork is laid down on the stem, the sori are formed and break through in the ordinary manner.

Sori on leaves and young stems are subcuticular to the extent that they arise in the cuticularized layer of the epidermal cells.

The teliospore buds grow out from the subterminal cells of the basal primordium, the terminal cells having become disorganized and swollen, functioning as buffer cells.

FRUIT DISEASE INVESTIGATIONS,
BUREAU OF PLANT INDUSTRY

EXPLANATION OF PLATE XXII

Gymnosporangium clavipes

FIG. 1. Longitudinal section of a part of a leaf at the edge of the vein. The mycelium is found principally in the upper epidermis from *a* to *e*. At *b*, *c*, and *d*, hyphae have invaded the mesophyll as shown by the darker regions.

FIG. 2. Section of infected branch of red cedar showing three regions containing mycelium.

FIG. 3. More highly magnified view of a portion of a similar section. The dark area between the leaf bases shows the limits of penetration.

FIG. 4. Section of a sorus on a larger limb; the mycelium beneath is confined to the region of the cork cambium. A fragment of the ruptured cork is seen at the left.

FIG. 5. Section from an infected area between two sori; the mycelium is likewise very superficial.

FIG. 6. Section of an infected stem similar to the one shown in figure 2, but made January 19th, the following winter. The old infected tissue has been cut off by wound callus (center above), and hyphae have grown in from the sides, attacking the cork cambium present only between the two leaf bases.

FIG. 7. Cross section at the edge of an infected leaf. The dark region indicates where the fungus is present. Cross sections of the hyphae are best shown in the cuticular layer.

FIG. 8. Surface view of a fragment of the cuticle with attached cuticularized layer raised above the sorus. Two kinds of markings: the outlines of the epidermal cells, and the corrosion pockets left by the hyphae or buffer cells of the sorus.